

CLASSIFICATION, SPORES, AND NOMENCLATURE OF THE MARSH FERN

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The Marsh Fern, *Thelypteris palustris*, represent one of the few species complexes in the ferns that occur on all of the large continents, and although absent from Australia, it is known from North Island, New Zealand. Several different taxonomic treatments have been based on diverse patterns of venation, the kinds and abundance of indument, and dimorphism of the leaves. However the diversity of these features has not been adequately reviewed over the broad geographic range of the species. Evidence from the surface and structure of the spore wall, pertinent to the classification, is presented here along with a reassessment of the classification and review of the nomenclature.

CLASSIFICATION

In the treatment of *Thelypteris palustris* by Fernald (1929), four varieties were proposed: var. *palustris* of Europe, the Caucasus, eastward to the Himalayas and southern China; var. *pubescens* of the northeastern United States and adjacent Canada and east Asia from Kamtchatka, Amur, and Manchuria; var. *Haleana* of the southeastern United States and Bermuda; and var. *squamigera* of southern India, Africa, and northern New Zealand. This last variety of the southern hemisphere has been treated as a species by Ching (1963) and Holttum et al. (1970). The varieties were assessed by A. Tryon (1971) with respect to morphological variation especially of the spores, and that study is extended here. Structural differences in the spore walls, especially the perispore, are evident in SEM studies, but the surface architecture is also apparent with the light microscope.

It is concluded that the Marsh Fern complex consists of two species, one largely of the southern hemisphere and the other, including two varieties, in the northern hemisphere.

METHODS AND MATERIAL

Whole, abraded, and sectioned spores were examined with an AMR 1000 scanning electron microscope at 20 KV. Specimens were fixed to stubs with doublesided adhesive tape and coated with gold-

palladium in a Hummer sputter coater for three minutes, depositing approximately 200 Å of metal. Spores were examined, with the light microscope, fixed in 85% lactic acid for an hour. In addition to the collections cited in the captions other specimens were studied with SEM or light microscope as listed under each of the taxa. Spores were obtained from collections in the Harvard University Herbaria or in the United States National Museum, cited as (US).

Thelypteris confluens

Spores of specimens from Africa, New Zealand and South America are echinate (Figs. 1, 3, 4, 5) and mostly larger than those of *T. palustris*. The African material has somewhat denser echinate elements but the irregularly granulate surface is similar to that of spores from Argentina (Figs. 3,4). A lower reticulate formation is not evident but may be obscured early in sporogenesis. The perispore is underlaid by a thick, dense exospore stratum (Fig. 2). In the work on spores of the South African ferns, Welman (1970) recognized *T. confluens* and described the spores as densely subechinate with spinules 1–2.5 μ long.

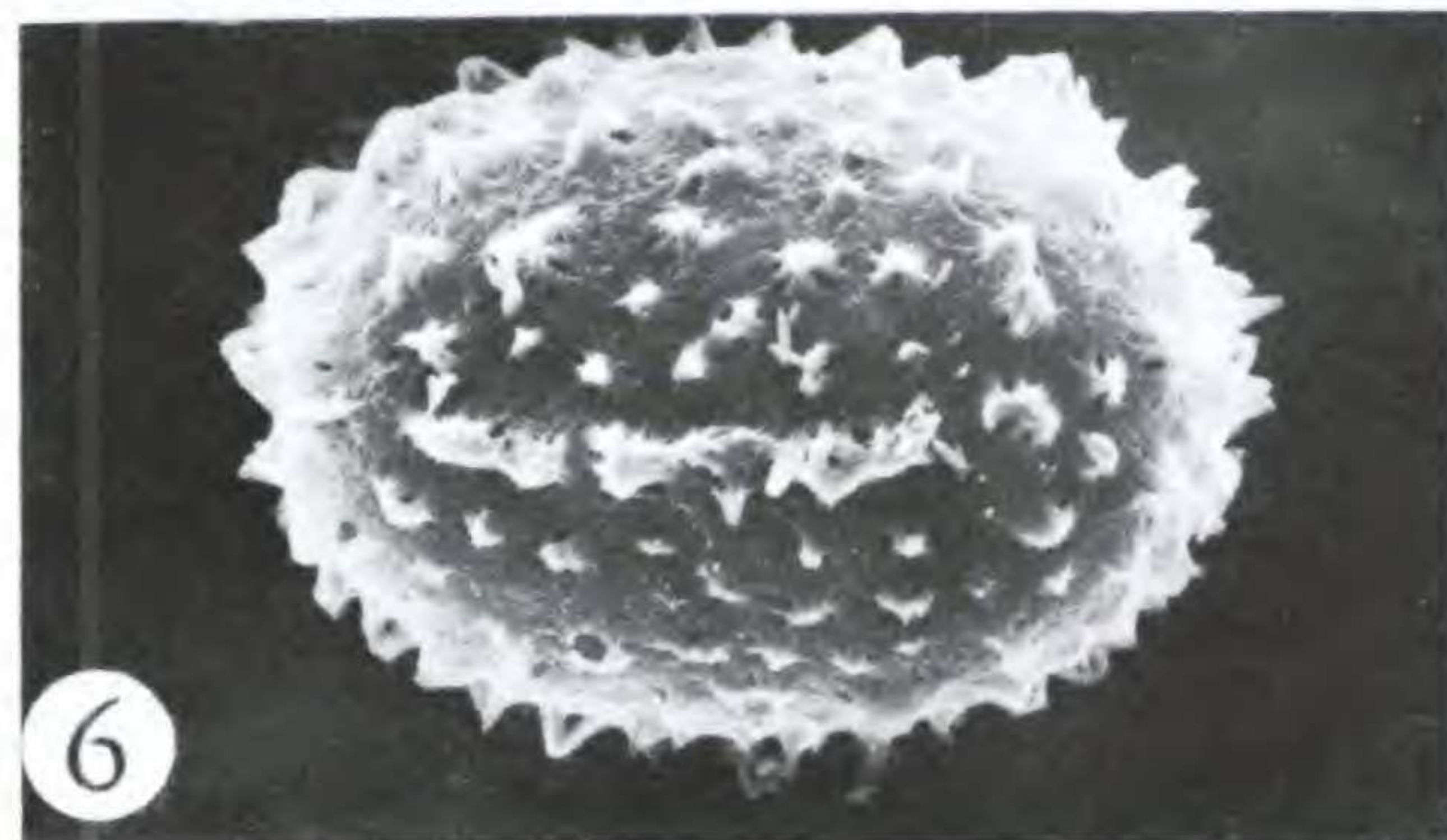
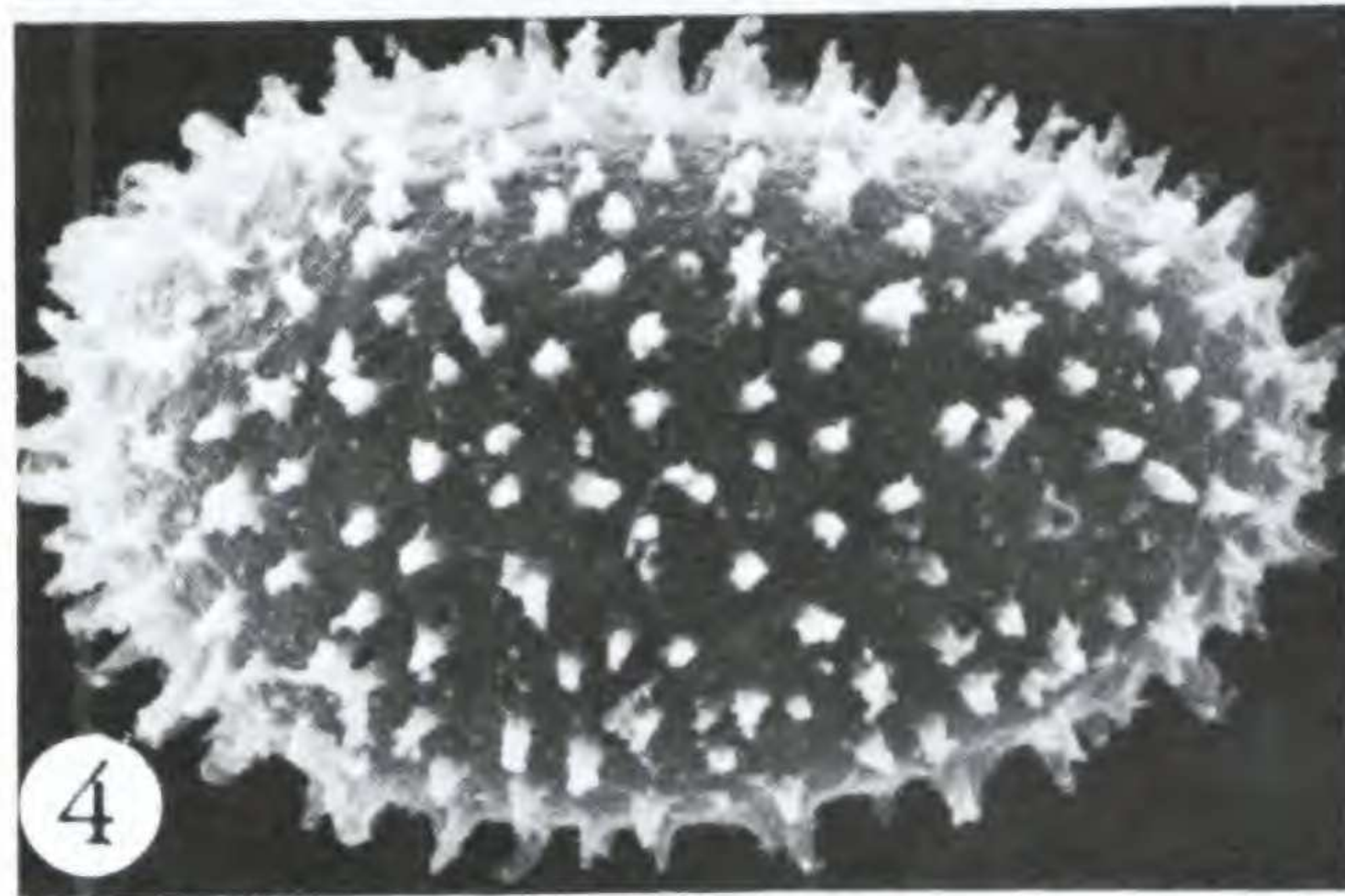
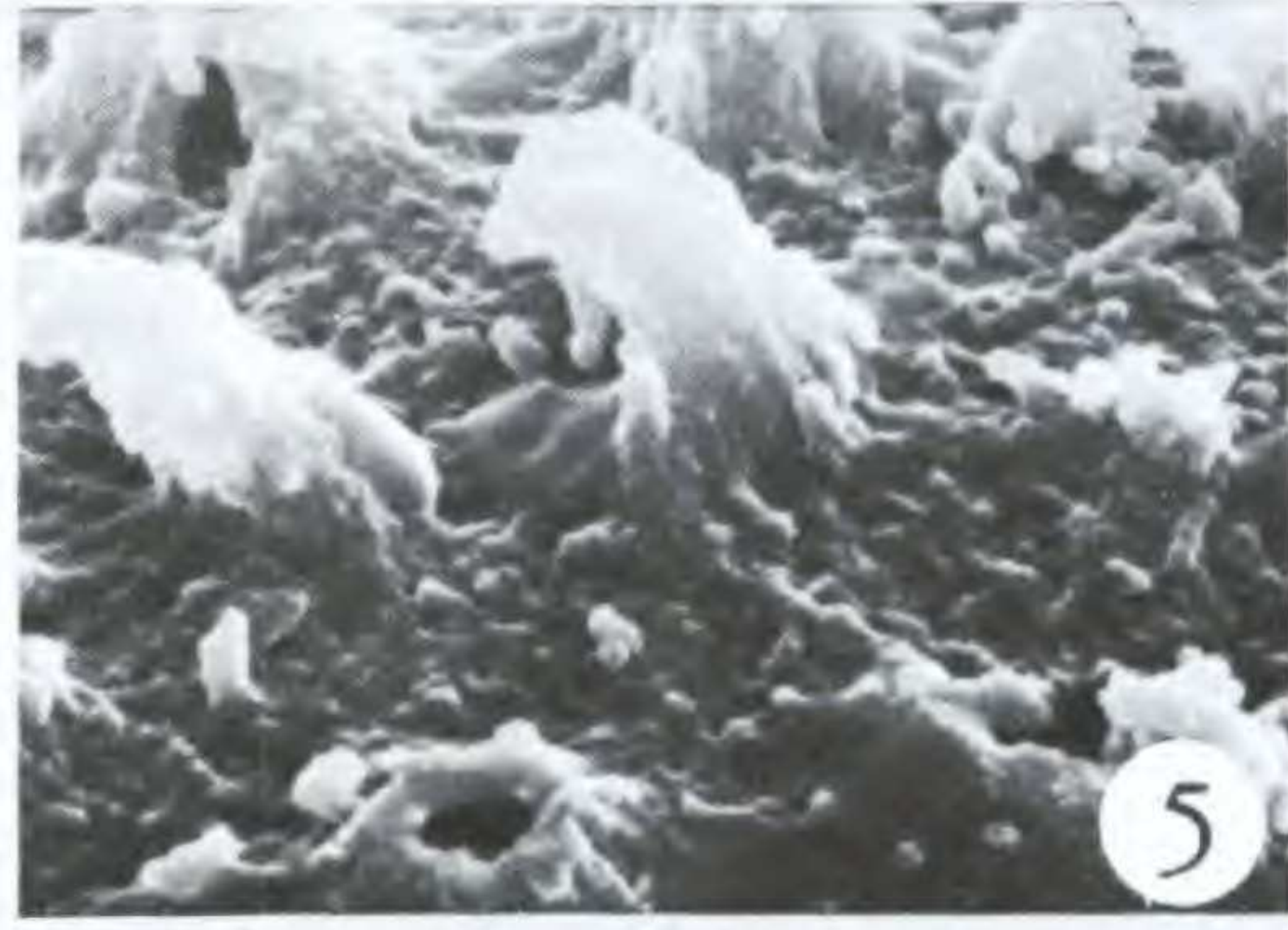
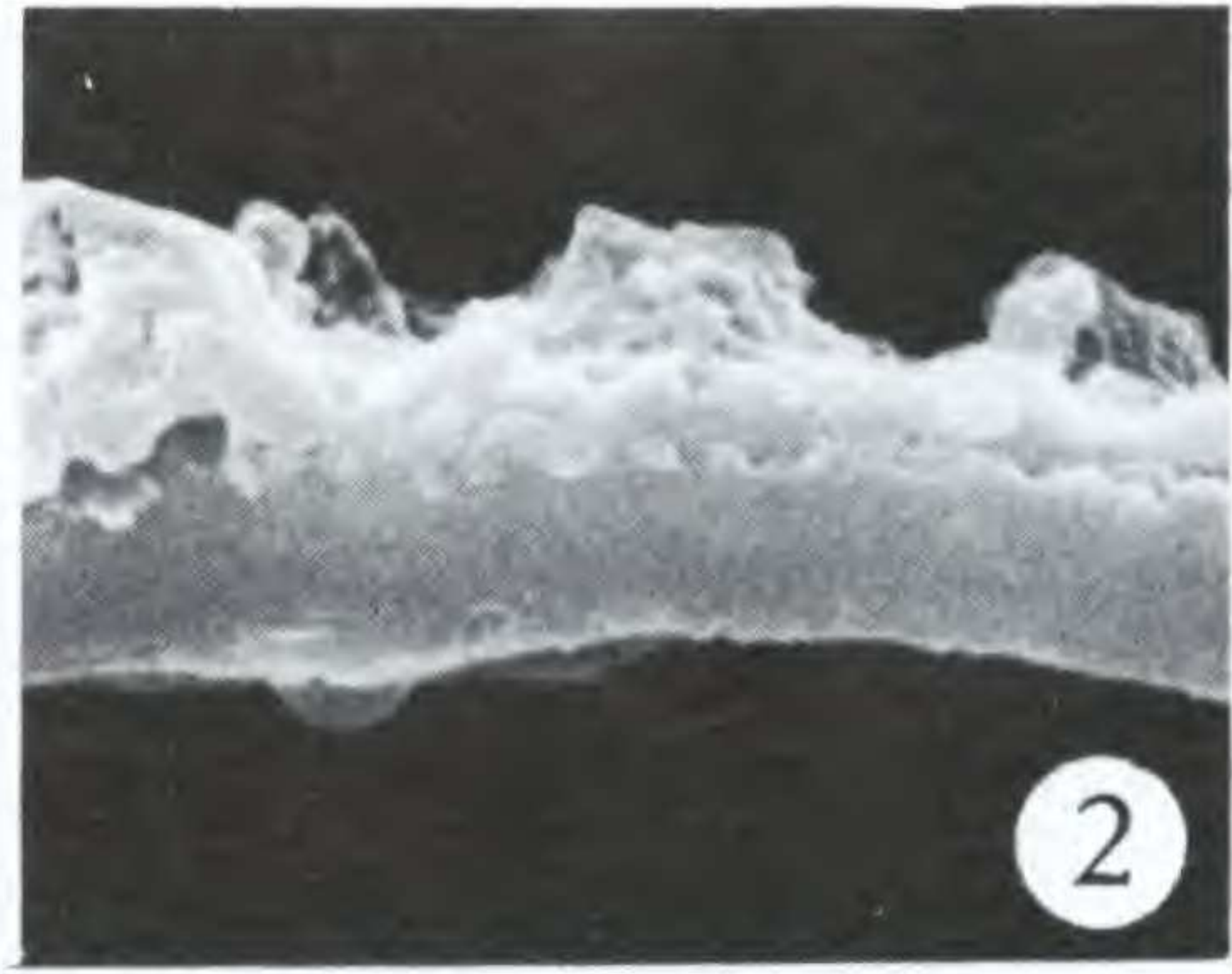
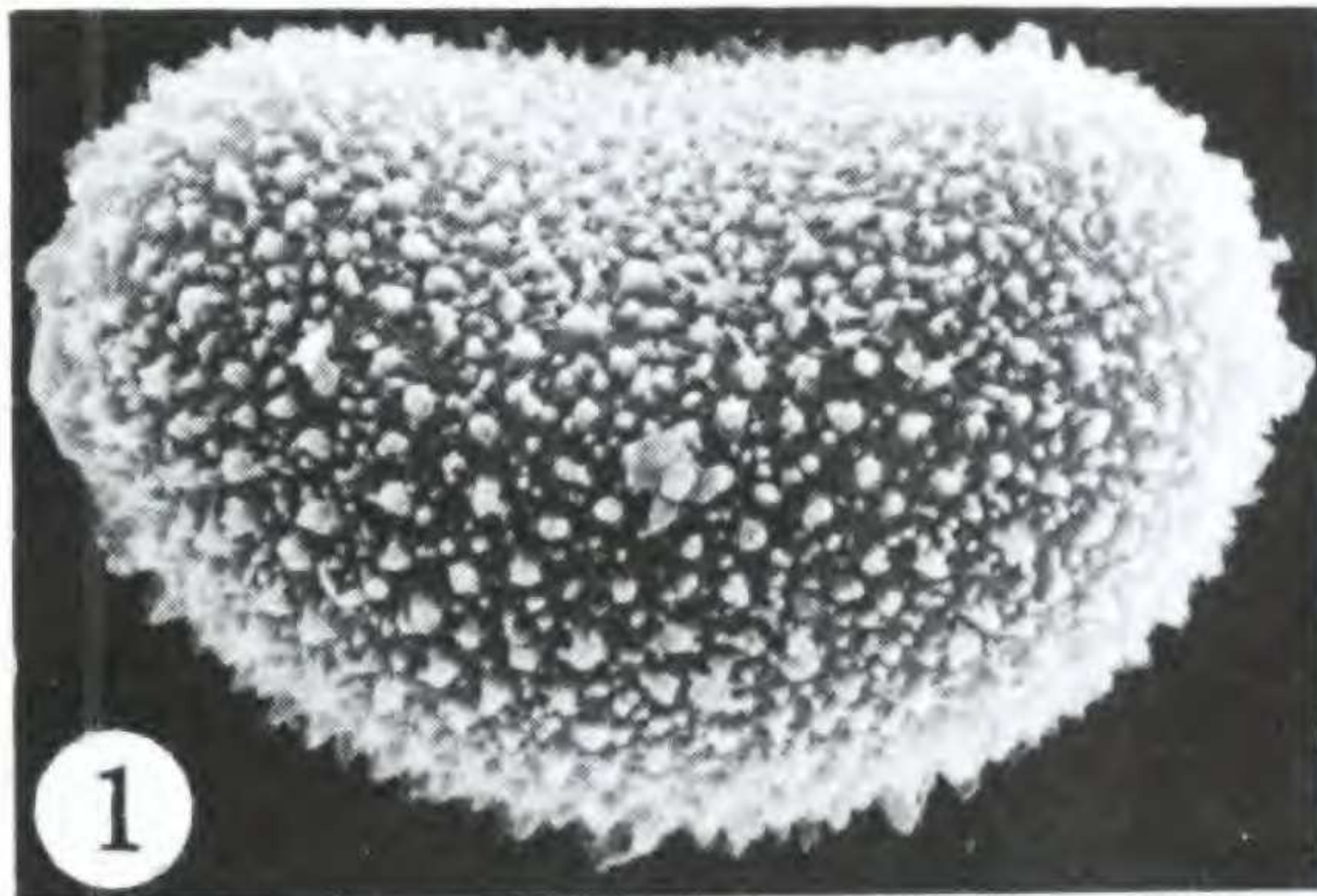
The costal scales of the lamina are a conspicuous feature of the leaves distinguishing *T. confluens* from *T. palustris*. In the latter species scales may occur, especially in young leaves, but they usually are caducous. The indusia have abundant trichomes or may be glandular.

Thelypteris confluens occurs in Africa, Madagascar, southern India, Burma, Sumatra, New Guinea, New Zealand, and South America. The American material, from northeastern Argentina, was described as *Dryopteris Cabrerae* Weatherby based on *Cabrera 10087*. Resemblance of this species to the Marsh Fern was noted in the original description, and echinate spores were indicated as an unexpected character distinguishing it from other species in the

Figures 1–7. *Thelypteris* spores.

1–5. *T. confluens*. 1–3. *Abraham 11*, Natal, Africa. 1. Densely echinate surface, $\times 1000$. 2. Wall profile, with eroded echinate perispore above thick exospore, $\times 10,000$. 3. Surface detail of echinate elements with granulate deposition, $\times 10,000$. 4,5. *Schulz 831*, Chaco, Argentina. 4. Spores with diffuse echinate elements, $\times 1000$. 5. Surface detail of echinate elements and granulate deposition, $\times 10,000$.

6,7. *T. palustris* var. *palustris*, *Ivanova 4297*, Kurgan, West Russia. 6. Proximal face with laesura at center, surface with projecting loops, $\times 1000$. 7. Wall profile (below) the spore interior with protoplast fragments at base, surface detail of reticulum (above), $\times 5000$.



group of *D. rivularioides*. Recognition of *T. confluens* as a species is reinforced by its austral geographical pattern known in other ferns as well as flowering plants.

Spores examined in additional collections are from: AFRICA. Uganda, *Longfield 65*; Tanganyika, *Drummond & Hemsley 2187*; South Africa, *Abraham 21*, *Buchanan 554 (US)*, *Burchell 4419*, *Taylor 677*. INDIA. Berijam Lake, *Jarrett & Saldanha 17054 (US)*. ARGENTINA. Buenos Aires, *Cabrera 10087*. NEW ZEALAND. Bay of Plenty, *Kirk; Craig*.

Thelypteris palustris* var. *palustris

The spores have a coarsely reticulate perispore, with prominent projecting loops, overlaying a thick exospore (Figs. 6, 7). The reticulate perispore is relatively uniform throughout the range as shown in collections from Honan Province, China (Chang, et al., 1976) as well as those included here from Europe. The wall consists largely of thick exospore below the reticulate perispore as in the wall profile, in the lower part of Fig. 7. The spores from Kashmir were treated under var. *squamigera* (= *T. confluens*) by A. Tryon (1971) but the strongly projecting loops clearly indicate that this belongs with var. *palustris*. Muir & Grant (1971) reported that spores of *T. palustris* treated with ultrasonic probe or acetolysis retained the reticulum but lost the projecting loops. The source of the spores was not given but they doubtless represent var. *palustris*.

Variety *palustris* usually has nearly monomorphic leaves with the veins mostly forked in the fertile leaf and the indusia have glandular trichomes. Plants are most readily distinguished from var. *pubescens* by these characters.

Variety *palustris* occurs in Europe eastward to central Asia, extending to China and south to Kashmir.

Spores examined in additional collections are from: EUROPE. Denmark, *Nielsen & Pedersen 508*; Germany, *Vocke* in 1884; Austria, *Petrack Exsic. 702*; Estonia, *Walter-Calle Exsic. 42*. USSR, Turgai (Kirgiz steppes), *Dubyabskii 1522*; W. Siberia, Tobolsk, *Mameev 597*. ISRAEL. *Eig & Feinbrun 728 (US)*. INDIA. Kashmir, *Thompson*.

Thelypteris palustris* var. *pubescens

Spores of this variety have a granulate or papillate to irregularly tuberculate or reticulate perispore similar to that of var. *palustris* but without prominent loops. Variation in the surface formation

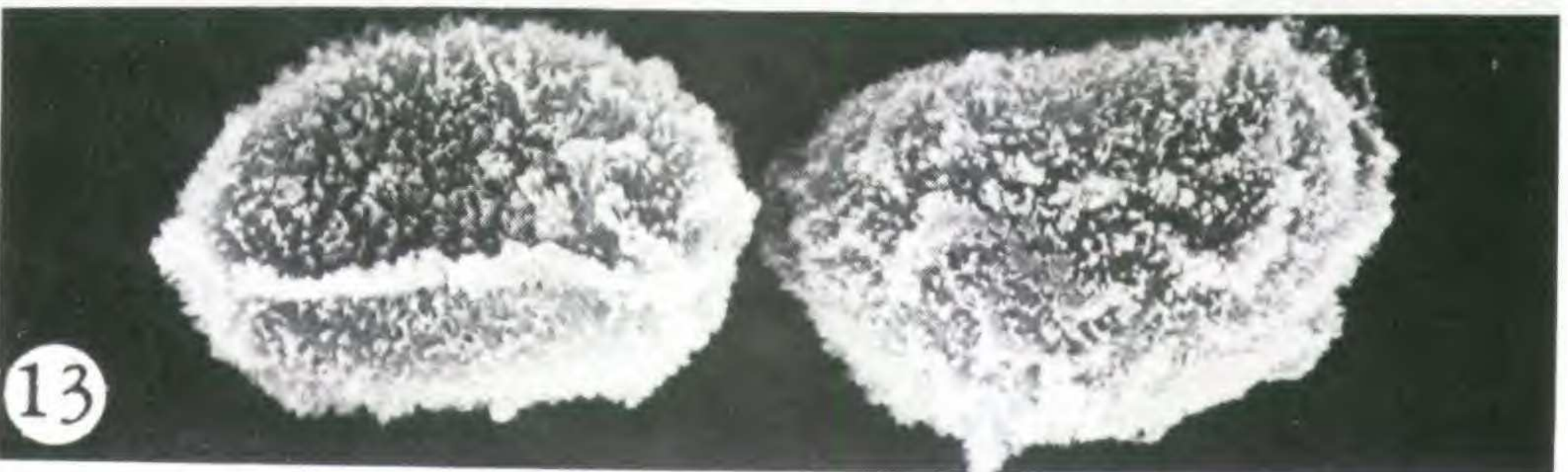
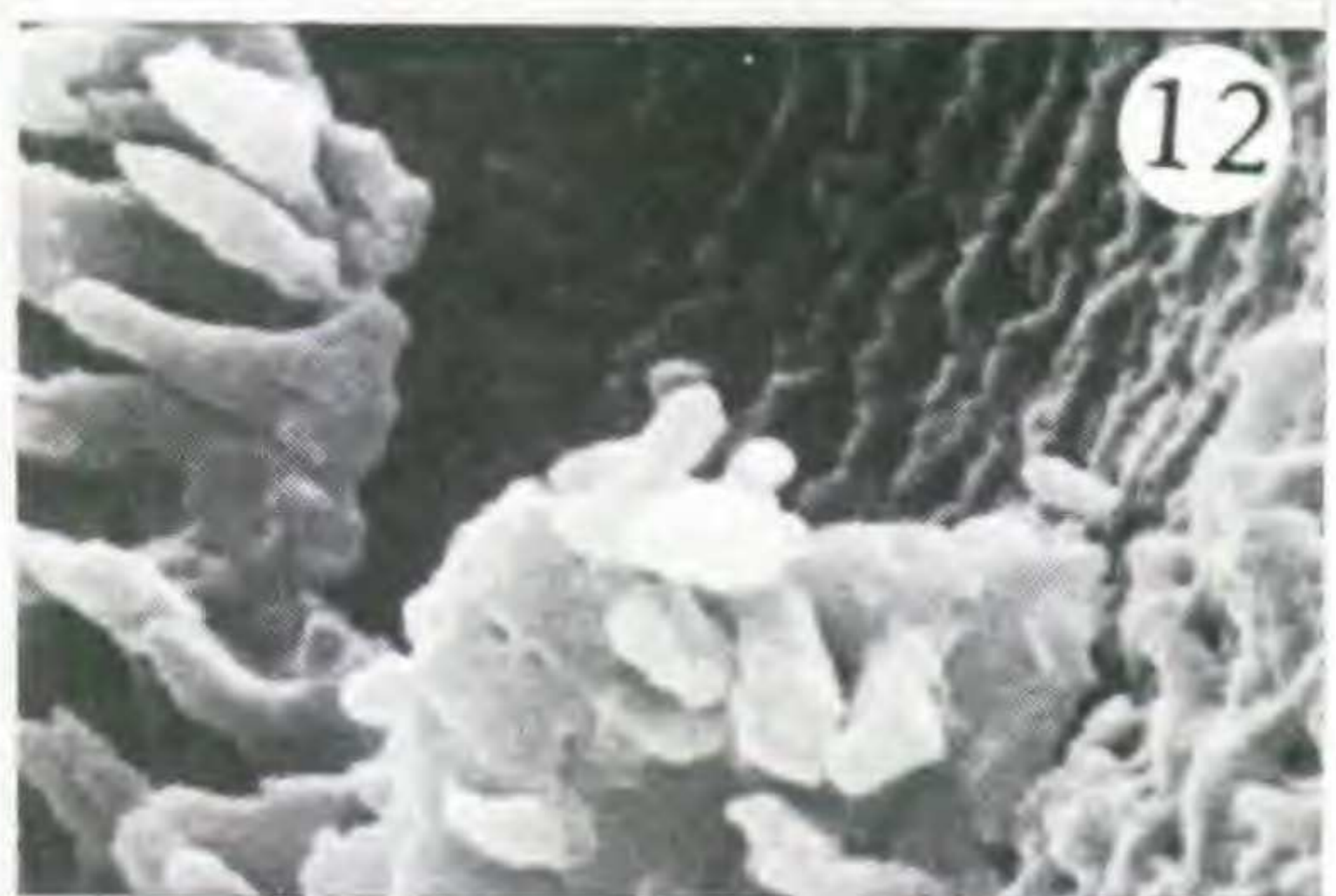
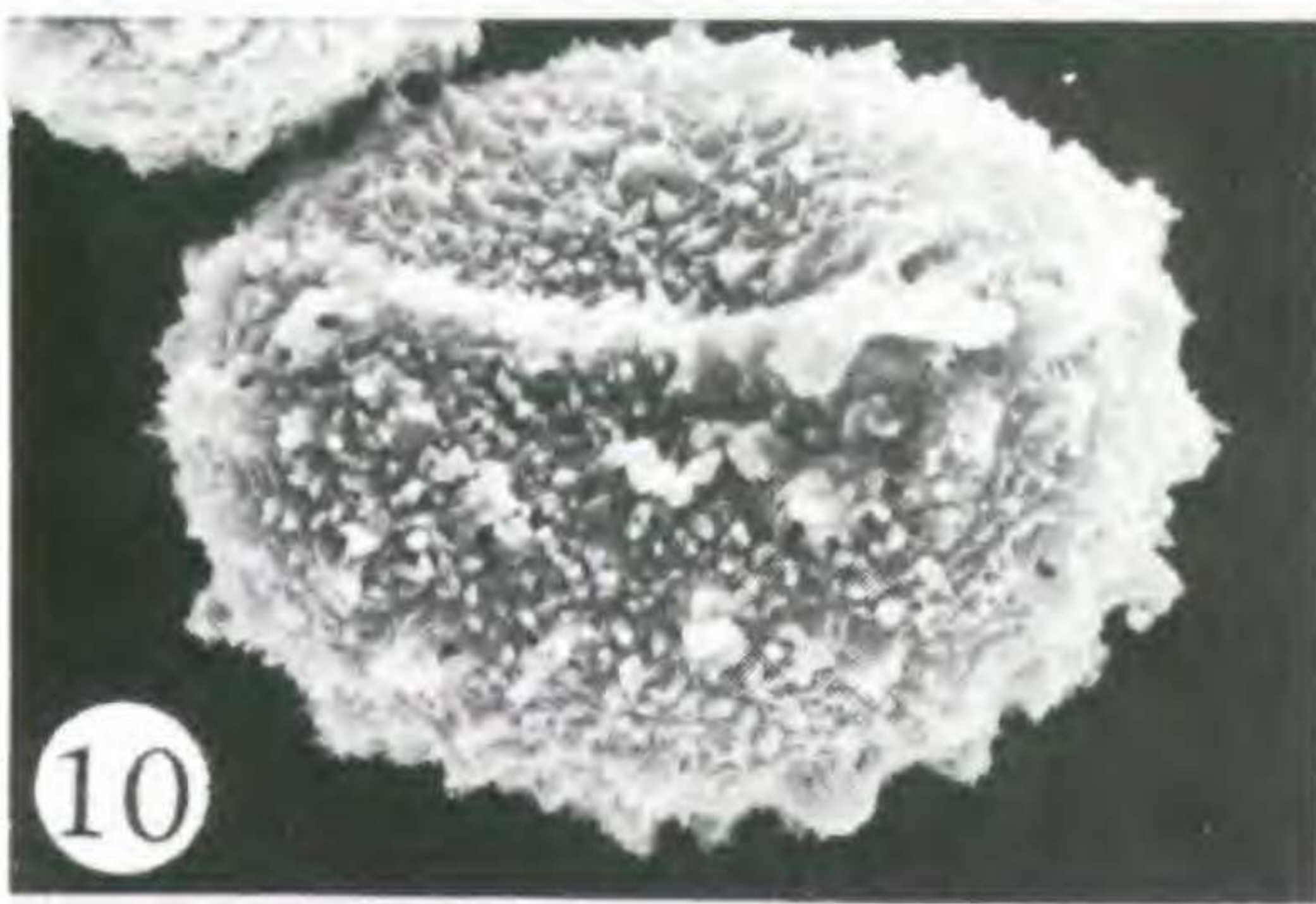
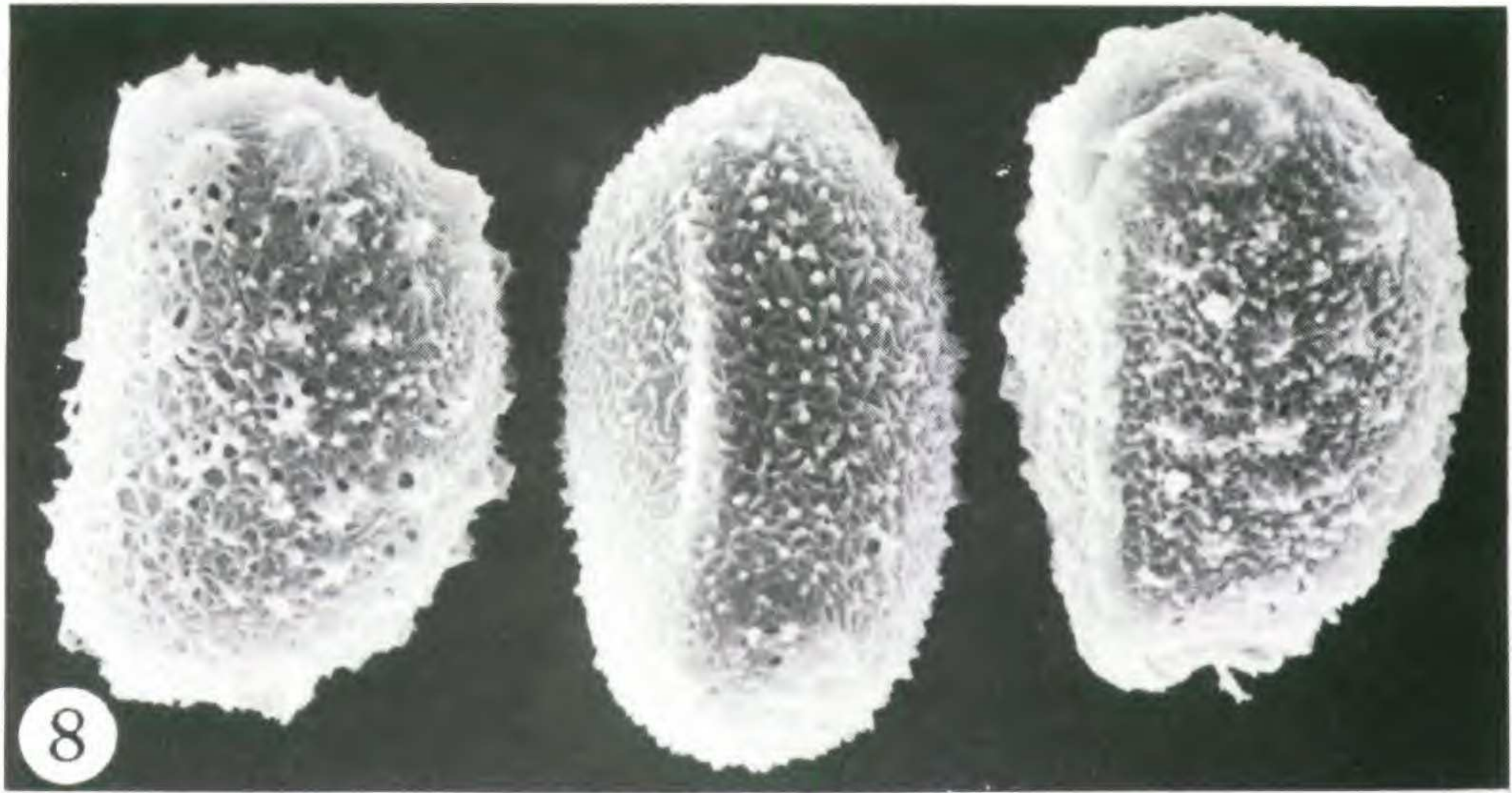
appears to relate to additions in deposition of the perispore. The surface variation in spores of a collection from Iowa (Tryon 1971, Figs. 2-5) is similar to that in three spores shown here from a Massachusetts specimen (Fig. 8). Each spore appears mature but varies in complexity of the surface. The central spore has the thinnest perispore of slender more or less protruding rods that barely cover the laesura. A more complex reticulum has developed on the spore at left. The spore at the right has the most elaborate perispore of dense papillate structure. Spores from Japan have a dense papillate surface but the basal reticulate formation is usually evident (Figs. 10, 11). Spores of collections from the southern United States also have a compact, papillate surface with a somewhat reticulate base (Figs. 12, 13) and the exospore beneath is finely rugose. The profile of a portion of the perispore lifted above the exospore (Fig. 9) shows the relatively thin perispore in this variety.

The leaves of var. *pubescens* are rather dimorphic, mostly with simple veins in the fertile leaves and the indusia are not or rarely glandular. Costal scales are usually absent but may persist in some specimens from the western part of the range in the United States. Material formerly distinguished as var. *Haleana* of the southern United States and Bermuda is included in var. *pubescens*, for this seems to encompass the same kind of variability as that in other plants of the latter variety. Variety *pubescens* occurs in the eastern United States and adjacent Canada, Cuba, Bermuda, Japan, and northeastern Asia.

Spores examined in additional collections are from: UNITED STATES. Maine, *Robinson 723*; Massachusetts, West Cambridge, without collector, in 1894, *A. Tryon 70-18*; Indiana, *R. Tryon 4404*; Iowa, *Pammel 579*; Nebraska, *Clements 293b*; Virginia, *Fernald et al. 4731*; Florida, *Bloomfield & Correll 6163*, *Lakela et al. 26990*; Louisiana, *Correll & Correll 9177*. CUBA. Habana, *Acuna y Linero 20068* (US). JAPAN. Hondo, *Furse*, in 1957, Honsyo, *Uno 24129*. USSR. Amur, *Maximowicz*, in 1855, E. Siberia, Vladivostock, *Topping 4510*.

COMENTS

The surface contour of these spores is formed by a relatively thin perispore overlaying a thick perispore. Spores of *Thelypteris confluens*, from widely disjunct areas of the southern hemisphere, are consistently echinate. A surface reticulum is not evident in mature



spores and the echinate elements as well as the basal surface consist of granulate material. Spores of *T. palustris* of the northern hemisphere are characterized by a reticulate surface that may be more or less obscured by additional papillate or granulate deposits. Specimens sampled over the range of var. *palustris*, across Eurasia to northern India, are uniformly reticulate. The considerable variation in spores of var. *pubescens*, especially in North America, appears to relate to the density in granulate deposit on the basal reticulum. Variation in spores of single collections of var. *pubescens* is similar to that within the range of the variety. The larger spore size in *T. confluens* suggests a possible higher ploidy level in the southern hemisphere elements of the complex than in the diploid *T. palustris*. There are no reports of chromosome numbers for *T. confluens*, although *T. palustris* has been widely sampled and is consistently $n=35$, in Europe, North America, and Japan.

NOMENCLATURE

Nephrodium thelypteroides Michaux has long been cited as a synonym of the New York Fern (= *Thelypteris noveboracensis*), for example, by Eaton (1879) and Christensen (1905). This usage was changed by Morton (1967) in his paper on the ferns of the Michaux Herbarium by the designation of a specimen of the Marsh Fern (= *Thelypteris palustris*) as the holotype of Michaux's name. The typification of Morton was accepted by Holub who adopted the name *Thelypteris thelypteroides* (Michaux) Holub for the northern element of the Marsh Fern. Since D. C. Eaton examined the Michaux collection in 1866 and arrived at a different conclusion, the typification was reinvestigated during a visit to the Museum National d'Histoire Naturelle in 1979.

Figures 8-13. *Thelypteris palustris* var. *pubescens* spores.

8,9. Churchill, in 1915, Berkshire Co., Mass. **8**. Three mature spores, the central one with more or less projecting strands or rods, the laesura vertical near center, the left spore with more complex reticulum, the right spore with papillate surface, the laesura at left, $\times 1000$. **9**. Wall profile with part of perispore lifted above the thick exospore, part of the spore interior with protoplast fragments (below) $\times 10,000$. 10,11. Serizawa 11041, Honshu, Japan. **10**. Spore slightly tilted with irregular papillate surface, the laesura horizontal, $\times 1000$. **11**. Detail of papillate surface, $\times 10,000$. 12,13. Correll & Correll 9177, Louisiana. **12**. Detail of abraded papillate surface raised above the exospore (at top), with a portion of the lower reticulate perispore structure at right, $\times 10,000$. **13**. Spores with dense papillate surface, proximal face with laesura (left), lateral aspect (right), $\times 10,000$.

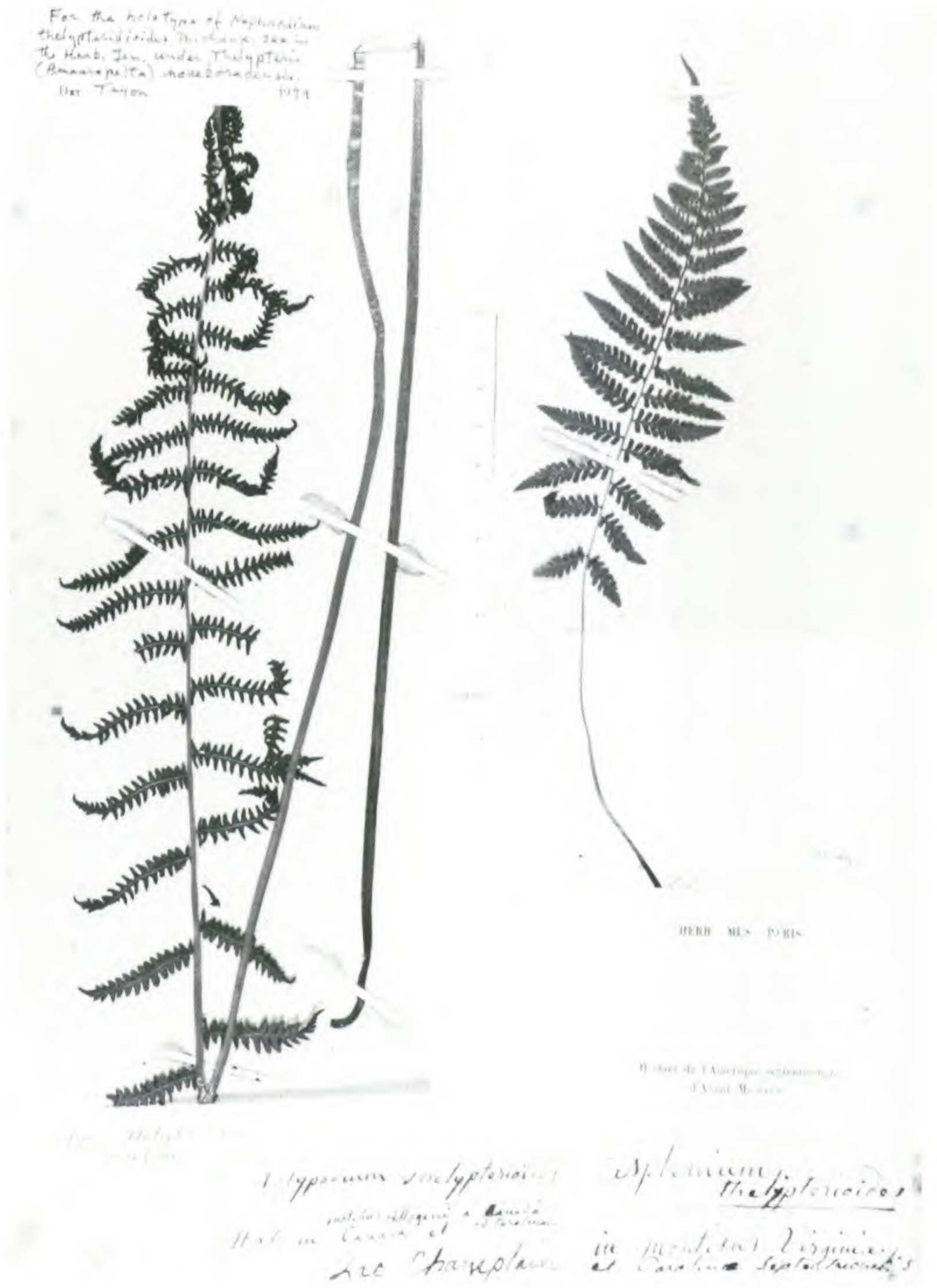


Figure 14. The specimen of “*Polypodium thelypteroides* Michaux” (left) in the Herbarium Michaux (= *Thelypteris palustris*). At right is a sterile leaf of another collection labeled *Asplenium thelypteroides*.

There are three sheets that pertain to the typification of *Nephrodium thelypteroides* Michaux, one in the Herbarium Michaux and two in the Herbarium General. The specimen in the Herbarium Michaux (Fig. 14), designated as the holotype by Morton, is named "Polypodium thelypteroides Michaux" and bears the data "Montibus Allegeni a Canada. Habitat in Canada et ad Carolinum. Lac Champlain." This specimen was annotated by D. C. Eaton in 1866 (Eaton, 1870) as *Aspidium thelypteris* Sw. and is clearly that species (= *Thelypteris palustris*). The locality data provided by Morton is incomplete, and he incorrectly indicated that the specimen is named *Nephrodium thelypteroides*.

In his *Ferns of North America*, D. C. Eaton (1879) cited *Nephrodium thelypteroides* as a synonym of *Aspidium noveboracense* (= *Thelypteris noveboracensis*), rather than of *Aspidium thelypteris*. This indicates that he did not accept the specimen of "Polypodium thelypteroides" that he had examined in the Herbarium Michaux as the type of that name. A second sheet in the Herbarium Richard and later in the Herbarium Drake (Fig. 15) bears a typical Michaux label with the data "Polypodium thelypteroides Michaux. Canada et in montib. Allegeni adusque Carol. montibus." It includes two leaves clearly of different gatherings. The third sheet (Fig. 16) includes two collections; one, two leaves at the left "Amerique Septentrionale, venant de Mr Comte par Boisduval. 1828." and the other, two leaves, at the right, with a note in the handwriting of Bory de St. Vincent: "donne par Richard comme de L'herbier Michaux, des Monts. Alleghani sous le nom de *Nephrodium thelypteroides*, 1808." The Michaux specimens on this sheet are identical to the right leaf on the Herbarium Richard sheet and are clearly of the same gathering. They are annotated, without date and in an unidentified script, as *Aspidium noveboracense*. All of these specimens are *Thelypteris noveboracensis*.

It is unfortunate that Morton overlooked these specimens in the general herbarium in his account of the Michaux material and did not recognize that Eaton had studied the specimen in the Herbarium Michaux prior to his publication of the *Ferns of North America*.

The Michaux specimens in the Herbarium Richard and the ones given to Bory are properly taken as the holotype of *Nephrodium thelypteroides* Michaux and they have been so annotated by Rolla Tryon. These specimens correspond to the Michaux protologue, especially to the contrast of the new species with the Marsh Fern



Figure 15. The Michaux holotype specimens of "Polypodium thelypteroides Michaux" in the Herbarium Richard (= *Thelypteris noveboracensis*).

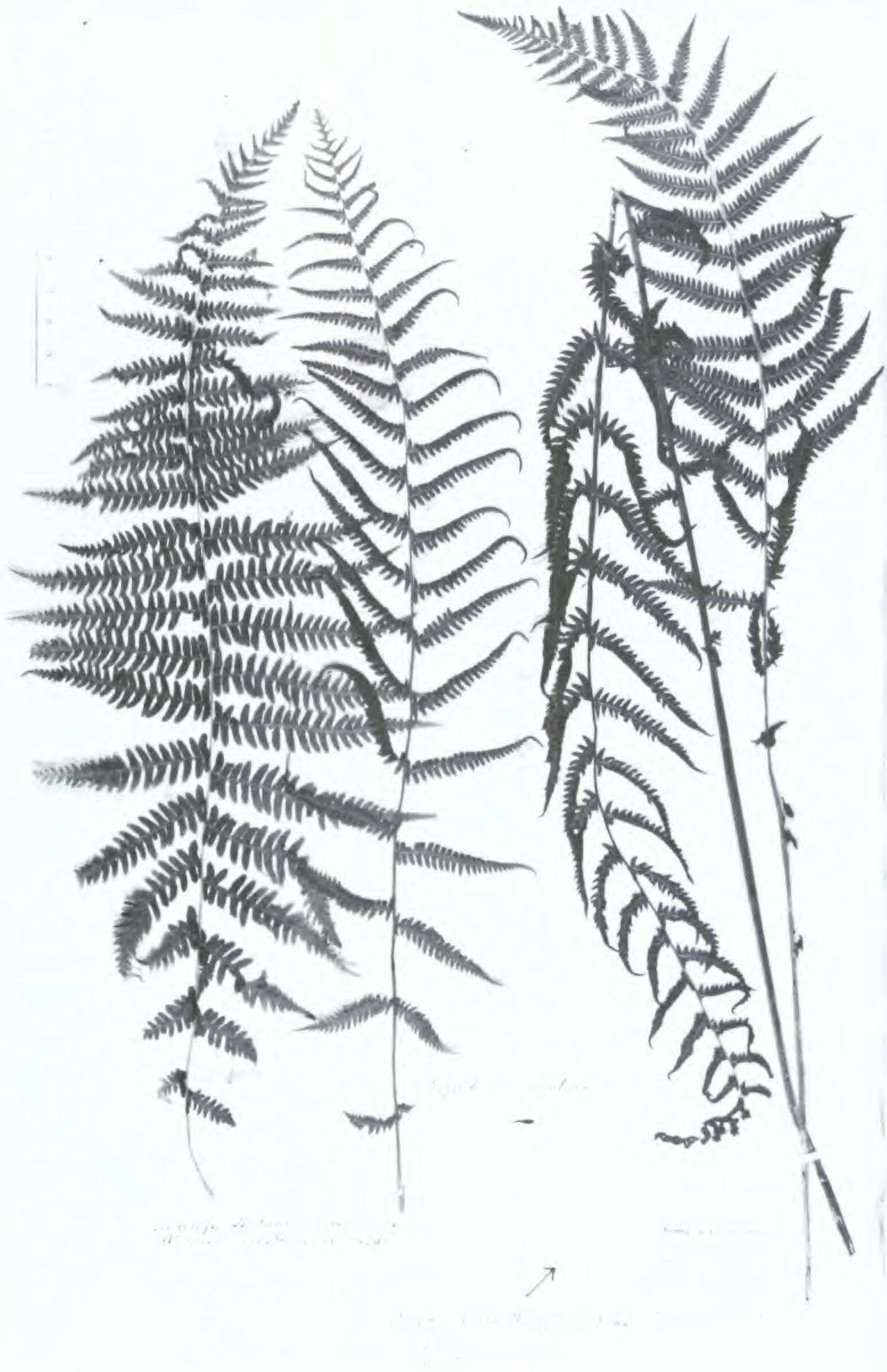


Figure 16. The Michaux holotype specimens of *Nephrodium thelypteroides* (right) given by Richard to Bory, in the Herbarium Bory (= *Thelypteris noveboracensis*). At left are two leaves of a later, different collection of the same species.

which was given as "Strongly allied to *Polypodium Thelypteris*; with the sori even at maturity not running together in that way." One of them bears the published name (slightly altered); and they also agree with the identity of the name as established by D. C. Eaton. The role of Richard in the publication of Michaux's *Flora Boreali—Americana* especially implicates the Herbarium Richard in the typification of Michaux names and supports the designation of holotype relating to his herbarium.

The essential nomenclature of the taxa discussed is as follows:

1. ***Thelypteris confluens*** (Thunb.) Morton, *Contrib. U.S. Nat. Herb.* **38**: 71. 1967.
Pteris confluens Thunb., *Prod. Fl. Cap.* 171. 1800.
Aspidium thelypteris var. *squamigerum* Schlect., *Adumbr.* **23**. 1825.
Nephrodium squamulosum Hook. fil., *Fl. N. Zeal.* **2**: 39. 1855.
Thelypteris palustris var. *squamigera* (Schlect.) Weath., *Contrib Gray Herb.* **73**: 40. 1924.
Thelypteris squamulosa (Hook. fil.) Ching, *Bull. Fan Mem. Instit. Biol. Bot.* **6**: 329. 1936.
Dryopteris Cabrerae Weath., *Bol. Soc. Argent. Bot.* **3**: 1949.
Thelypteris Cabrerae (Weath.) Abbiatti, *Rev. Mus. La Plata (Bot.)* **9**: 19. 1958.

2. *Thelypteris palustris* Schott, *Gen. Fil. adnot. t.* 10. 1834, *nom. nov.* for *Acrostichum thelypteris* L. (*Aspidium thelypteris* (L.) Sw.)
 - 2a. ***Thelypteris palustris*** var. ***palustris***
Acrostichum thelypteris L., *Sp. Pl.* 1071. 1753.
Polypodium pterioides Lam., *Fl. Franc.* 1: *Meth. Anal.* **18**. 1778, *nom. superfl.* for *Acrostichum thelypteris* L.
Polypodium palustre Salisb., *Prod.* 403. 1796, not Burm. 1768.
Aspidium palustre S. F. Gray, *Nat. Arr. Brit. Pl.* **2**: 9. 1821, *nom. superfl.* for *Acrostichum thelypteris* L.
Thelypteris thelypterioides ssp. *glabra* Holub, *Taxon* **21**: 332. 1972.
 - 2b. ***Thelypteris palustris*** var. ***pubescens*** (Lawson) Fernald, *Rhodora* **31**: 34. 1929.

- Lastrea thelypteris* var. *pubescens* Lawson, Edinb. New Philos. Journ. n.s. **19**: 277. 1864, reprint as Syn. Canad. ferns filicoid plts. **21**. 1864; also Trans. Bot. Soc. Edinb. **8**: 38. 1864.
- Thelypteris palustris* var. *Haleana* Fernald, Rhodora **31**: 34. 1929.
- Thelypteris confluens* var. *pubescens* (Lawson) Pringle, Roy. Bot. Gard. (Ontario) Tech. Bull. **4**: 42. 1969.

3. ***Thelypteris noveboracensis*** (L.) Nieuwl., Amer. Midl. Nat. **1**: 226. 1910.
- Polypodium noveboracense* L., Sp. Pl. 1091. 1753.
- Nephrodium thelypterioides* Michaux, Fl. Bor. -Amer. 267. 1803.
- Thelypteris thelypterioides* (Michaux) Holub, Taxon **21**: 332. 1972.

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Discussion of *Thelypteris* with Alan R. Smith, preliminary to this study, and his comments on the manuscript have been most helpful. We are most appreciative of the SEM work of Edward Seling at the Museum of Comparative Zoology, Harvard University. The assistance of Gerald J. Gastony with the translation of Michaux's protologue is gratefully acknowledged. The spore studies are supported by NSF Grant DEB 78-03148 to Rolla and Alice Tryon.

LITERATURE CITED

- CHANG Y. L., I. C. HSI, C. T. CHANG, K. C. KAO, N. C. TU, H. C. SUN, and C. C. KUNG. 1976. Spora Pteridophytorum Sinicorum. Botanical Institute Academia Sinica, Science Press. Peking. 451 pp., 89 plates.
- CHING, R. C. 1963. A reclassification of the family Thelypteridaceae from the Mainland of Asia. Acta Phytotaxonomica Sinica **8**: 289-335.
- CHRISTENSEN, C. 1905. Index filicum, p. 451. Hafniae, Hagerup.
- EATON, D. C. 1870. Notes on some of the plants in the herbaria of Linné and Michaux. Canad. Nat. **13** (n.s. 5): 24-31.
- . 1879. Ferns of North America. Vol. 1. Cassino, Salem, Ma. 352 pp.
- FERNALD, M. L. 1929. A study of *Thelypteris palustris*. Rhodora **31**: 27-40.
- HOLTUM, R. E., U. SEN, & D. MITRA. 1970. Studies in the family Thelypteridaceae 2. A comparative study of the type species of *Thelypteris* Schmidel, *Cyclosorus* Link, and *Ampelopsis* Kze. Blumea **18**: 195-215.
- MORTON, C. V. 1967. The fern herbarium of André Michaux. Amer. Fern Jour. **57**: 166-182.

- MUIR, M. D. & P. R. GRANT. 1971. Application of Scanning electron microscope techniques and optical microscopy to the study of sporopollenin, 422-439, *In*: J. Brooks, Ed., Sporopollenin, Proceedings of a Symposium, Geology Dept. Imperial College. Academic Press. London. 718 pp.
- TRYON, A. F. 1971. Structure and variation in spores of *Thelypteris palustris*. *Rhodora* 73: 443-460.
- WELMAN, W. G. 1970. The South African fern spores, *In*: E. M. Van Zinderen Bakker, Ed. South African Pollen Grains and Spores 6. A. A. Balkema. Cape Town. 110 pp.

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